



Highlighting the importance of water availability in reproductive processes to understand climate change impacts on plant biodiversity

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ABSTRACT

Drought sensitivity is known to affect plant species distribution. However, since every stage of plant life cycle has its own water requirements, plant performance and productivity is largely influenced by the timing of water stress. Variation in drought sensitivity between stages might explain recently observed changes in tree age structure along environmental gradients as well as species-specific responses to drought, yet it has poorly been taken into account in species distribution models (SDMs). In this paper we discuss how plant responses to water availability during various life stages influence species distribution and abundance. We define the role of water availability at the stage of gametophyte, zygote, seed and seedling and explain the nature of drought-related injuries. Moreover, we review examples that illustrate how plants adjust their phenology to cope with water stress at early stages of plant life cycle. We also discuss possible ways forward of incorporating the effect of water availability on different stages of the reproductive cycle into correlative and process-based plant species distribution models (SDMs) in order to improve the accuracy of their predictions.

1. Introduction

During the 21st century, a predicted decline in precipitation as well as an increase in potential evapotranspiration are expected to trigger severe and more frequent drought events in sub-tropics, Amazon region, western North America as well as the Mediterranean environments (Allen et al., 2010; Cook et al., 2014). The inability of woody species to recover from water stress may induce local extinction, alter forest composition and trigger the grassland spread towards regions currently covered in forests. Between 1987 and 2007 drought events on the Iberian Peninsula have already triggered changes in crown structure, defoliation percentage and forest dieback (Carnicer et al., 2011). Long and severe summer drought across Europe in 2003 has also been linked to increases in tree mortality rates in temperate mixed conifer and broadleaf forests of France (see for review Allen et al., 2010). In order to prevent severe species decline following these events, drought-induced adult mortality should be compensated by good seed production and high seedling recruitment rates (Lloret et al., 2009). Nonetheless, projected reduction in rainfall might negatively affect the success in early-life cycle stages and only increase the gap between the adult mortality and regeneration. Therefore, in order to predict vegetation responses to water stress it is crucial to look at life stages undergone by a plant before it reaches maturity. Plant sensitivity to

various environmental drivers may vary at each of this stage and can significantly affect species fitness, and thus species distribution.

As every life stage has its own water requirements and thresholds, their identification and quantification are necessary prerequisites for understanding how such constraints may limit species distribution. The effects of limited water supply on plant fitness can also vary between species of the same community at the particular life stage. In this paper we will discuss how the plant response to water availability during various stages of the life cycle influences the abundance and distribution of seed plants that represent the largest plant group found in all forest ecosystems. We will also suggest possible ways of incorporating drought sensitivity of early life stages into species distribution models and will discuss phenological adjustments at different stages of the reproductive cycle.

2. Plant life stages and their sensitivity to water availability

2.1. Gametophyte stage

Reductions in carbohydrates influxes, associated with low photosynthetic activity, as well as abscisic acid (ABA) accumulation in reproductive organs are suggested to be the major reasons for male and female gametophytic sterility (Fig. 1). Notably, however, male

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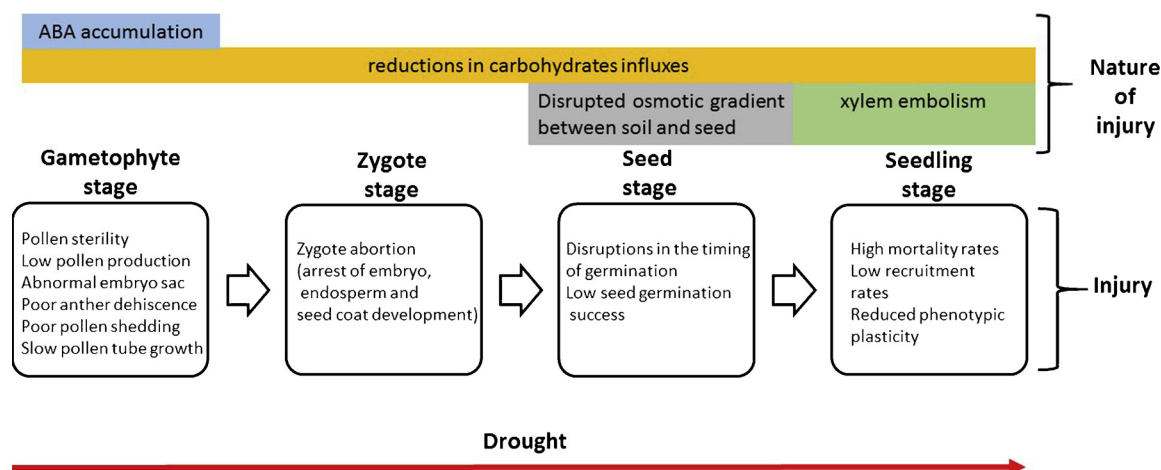


Fig. 1. Impact of drought on early life stages and nature of these effects.

gametophytes are generally more sensitive to water stress than the female ones (Saini et al., 1984). This damage is particularly severe if drought coincides with meiosis in anthers (Saini and Westgate, 2000). Studies on reproductive responses show that low water availability triggers pollen sterility in cereals, like rice, wheat, sorghum, barley, oat and maize, as well as in long-lived woody species, like holm oak (e.g. Bykova et al., 2018). Sterile anthers developed under the drought conditions are usually smaller, thinner and deformed (Sheoran and Saini, 1996). Aside from pollen sterility, water stressed plants regularly experience reductions in pollen production (number of pollen grains per anther) as well as poor anther dehiscence, deficient pollen shedding and slower pollen tube growth (e.g. Kelish et al., 2014; Bykova et al., 2018).

Although the female gametophytes are reportedly less sensitive to short-term drought conditions, prolonged and strong water stress is still able to affect their development which, unlike male sterility, cannot be offset by cross-pollination from less affected florets/flowers (Saini, 1997). The impairment of female gametophytes and associated reductions in grain yield were demonstrated in corn plants subjected twice to the drought stress during a 10-day period which coincided with the embryo sac formation. Almost 50% of embryo sacs developed under these stress conditions were abnormal (Moss and Downey, 1970).

2.2. Zygote stage

After fertilization and during zygote formation the effect of dehydration could also be detrimental. Only a few days of exposure to the water stress, during or shortly prior to this stage, result in reductions in starch reserves and sucrose supply and can trigger abortion of newly formed zygotes (Zinselmeyer et al., 1999). Westgate and Boyer (1986) reported reproductive failure of maize grown under reduced water supply for several days and attributed it to zygote abortion. Controlled environment experiments demonstrated that despite good pollen germination rates and successful egg sac fertilization, maize plants failed to develop an embryo, endosperm as well as seed coat and did not produce grains. The authors proposed that drought-induced reductions in photosynthetic activity (initiated during the gametophyte stage) resulted in low photosynthate influx and inability of zygotes to complete their development (Westgate and Boyer, 1986). Detrimental effect of summer drought on seed production, coinciding with zygote stage, has also been demonstrated in Mediterranean oaks (*Quercus ilex* and *Q. humilis*) (Espelta et al., 2008; Perez-Ramos et al., 2010). However, further experimental manipulations are still required to identify whether the observed reductions in acorns production were due to drought-induced zygotic abortion and not to other cell disruptions during the seed stage.

2.3. Seed stage

The timing and success of seed germination are regulated by a large number of abiotic factors, including water availability, temperature, oxygen concentration and light. Drought stress imposed during the process of seed formation, particularly seed filling phase, was found to affect the accumulation of assimilates, like water soluble carbohydrates, in the seed and influence its size and overall quality (Alqudah et al., 2011). Seeds developed under drought conditions can have reduced endosperm cell number and, as a result, lower weight (Singh and Jenner, 1982). Besides, the alternation of seed hormonal balance (i.e. decreases in Gibberellic acid (GA), increases in Absciscic acid (ABA)) accelerates the rate of seed filling, decreases its duration and significantly reduces the seed yield (Munier-Jolain et al., 1998; Yang et al., 2001). Although severe drought stress during seed filling was found to have little effect on soybean germination, it was able to reduce its yield by almost 40% (Vieira et al., 1991).

2.4. Seedling stage

Adult plants of a species may be able to tolerate a much wider range of climatic conditions than seedlings. Seedling root system is always less developed than that of adults, which makes seedlings more susceptible to water stress. Besides, dynamic responses of adult plants often differ from the ones of seedlings with different species exhibiting distinct responses to drought conditions (Lloret et al., 2009). Seedlings of *Quercus ilex*, for example, were shown to be less sensitive to water stress than seedlings of *Phillyrea media*, while the adult individuals of these species showed an opposite ranking (Lloret et al., 2004). In addition, even species within the same genus can have distinct seedling sensitivities to drought and therefore will react differently to projected changes in precipitation regimes. The results of a common garden experiment revealed that seedlings of *Pinus sylvestris* and closely related *Pinus nigra* from the Mediterranean region had higher emergence and lower mortality rates under the drought conditions than seedlings of *P. sylvestris* from the continental Central Alps (Richter et al., 2012). It was also demonstrated that seedlings that emerged from seeds collected from the southern populations of *P. sylvestris* developed higher root biomass, longer taproots and possessed higher phenotypic plasticity under the drought conditions (Taeger et al., 2015). These results suggest that the projected reduction in precipitation will have more pronounced effect on seedling recruitment in Central Alps than in the Mediterranean region.

Table 1
Drought adaptations during early life stage in seed plants.

Life stage	Phenological adaptation	Reference
Gametophyte	Early flowering and early anthesis	Brachi et al., 2012; Wolfe and Tonsor, 2014
Zygote	Zygote dormancy and associated extended zygote stage	Evenari, 1984; Liu et al., 2008
Seed	Shorter seed stage due to early germination. Extended seed stage due to seed dormancy or 'seed hydration memory' phenomenon	Brachi et al., 2012; Karimmojeni et al., 2014 Dubrovsky, 1996
Seedling	Early seedling emergence, due to short lag phase between germination and emergence Short phenophase for growth that occurs before the onset of severe drought	Castro, 2006 Perez-Ramos et al., 2013

3. Phenological adaptations at different life stages

One way to overcome drought stress is to adapt phenologically by shifting the occurrence of the most sensitive life stages to periods with higher water availability. In order to maximize fitness in dry environments, seed plants can shorten their life cycles (annuals), reduce the length of their life stages or shift the timing of a particular stage (Table 1). Strategies commonly employed to escape drought during the first life stage are either earlier flowering or reductions of the flowering period. It was reported that lineages of *Arabidopsis thaliana* collected at dry low-elevation sites exhibited earlier bolting, earlier flowering and higher fitness in comparison with high-elevation lineages (Wolfe and Tonsor, 2014). Another study demonstrated that plants of *A. thaliana* exposed to limited water conditions 32 days and 39 days after sowing showed a delayed flowering, but shorter flowering duration (Brachi et al., 2012). Differences in these responses might be associated with the extent of the water stress and variability in biomass distribution.

Unlike the gametophyte stage, phenological adjustments during the zygote phase are not well studied. However, it is possible that zygote dormancy could serve as an important drought adaptation strategy. While in most species the zygote transforms into an embryo without substantial delays, in some, like *Pistacia vera*, they can remain 'dormant' between fertilization and first division up to several months or even a year which might increase species chances for survival during the drought stress (Evenari, 1984). It was reported that in *Tapiscia sinensis*, for instance, the fertilization process usually occurs in May; nonetheless, the newly formed zygotes can instantly go into dormancy and remain dormant until the beginning of next flowering period (Liu et al., 2008).

Another phenological adaptation to limited water supply is early germination which can be related to maternal environmental effects as well as to a specific genetic strategy. Environmental conditions experienced by plants during seed maturation and after its dispersal largely determine the timing of germination and affect species fitness. For example, the seeds of *Amaranthus retroflexus* developed under limited water supply showed weaker dormancy, higher germination percentage and improved germination rate (Karimmojeni et al., 2014). Nonetheless, the seed stage can also be extended by the delay in germination timing. In order to survive drought, germinate and increase seedling chances for survival under the conditions of discontinuous hydration and dehydration, some arid species, like cacti, develop an adaptation so-called 'seed hydration memory' (Dubrovsky, 1996). This phenomenon is associated with species ability to maintain physiological changes that occurred during the first hydration period and germinate after prolong drought events. Ramírez-Tobias et al. (2014) demonstrated that seeds of most *Agave* species are able to maintain 70% hydration for up to 30 days and germinate upon the arrival of adequate soil moisture conditions.

Early seedling emergence associated with earlier germination or/and reduced lag phase between germination and emergence is used by species to increase seedling survival during drought. Seedlings of *Pinus sylvestris* at its southern distribution range, for example, emerge earlier in the season increasing their chances for establishment (Castro, 2006). Another drought-avoidance phenological strategy at the seedling stage is a shorter growth phase that ceases before the onset of severe drought.

Quercus ilex, which seedlings largely depend on seed reserves, uses this strategy to cope with summer water deficit (Perez-Ramos et al., 2013). Although matching phenology with water availability is not a rare phenomenon, the ability of plants to adjust the timing of their developmental processes is limited. The less phenotypically plastic is the functional trait associated with a certain life stage, the more constrains it puts on species distribution in a changing world.

4. Early life-stage functional traits and species distribution in a changing climate

Projected increases in frequency, duration and intensity of drought events might severely alter plant community composition and affect distribution ranges due to species-specific differences in early life-stage functional traits. Therefore, the analysis of these traits and their responses to drought should allow obtaining more accurate projections of species distribution in future climatic conditions. Species-specific differences in early life-stage functional traits can predict changes in forest community composition as well as community composition trajectories. High rooting depth per leaf area ratio, slow relative growth and low assimilation rates at the seedling stage in Mediterranean woody species (e.g. *Quercus ilex*, *Quercus suber*, *Pinus pinea*), for example, were shown to be associated with species ability to survive droughts (Lopez-Iglesias et al., 2014). Moreover, the possession of specific hydraulic traits has also been linked to the differential survival among tree seedlings under the limited water supply. Tyree et al. (2003) found that in five species from Central Panama (*Virola surinamensis*, *Calophyllum longifolium*, *Ouratea lucens*, *Dipteryx panamensis*, *Licania platypus*) seedling drought survival correlated with leaf water content, leaf water potential, and whole-stem hydraulic conductance. Seedlings with higher survival ratios were characterized by a more negative leaf water potential and lower xylem vulnerability to cavitation.

Seed desiccation sensitivity, another functional early life-stage trait, might play one of the central roles in regulating plant community composition in response to climatic changes. Desiccation-sensitive, also known as non-orthodox, seeds, maintain continuous metabolism, shed with high moisture content and are able to germinate shortly after release (Joët et al., 2013). This type of seeds is largely produced by tree and shrub taxa (Tweddle et al., 2003) which might determine their recruitment success and make them vulnerable to predicted decreases in precipitation (Joët et al., 2013). If this happens, non-orthodox seed species will be outcompeted by herbaceous species that generally produce less drought-sensitive seeds and are also known to exhibit various drought survival strategies (Balachowski et al., 2016). Unlike woody species, herbaceous are usually controlled by seed germination and emergence. Their drought survival, as it was demonstrated during the experiment with 47 varieties of dryland grasses (Larson et al., 2015), is related rather to the coleoptile tissue density than other functional traits associated with early life stages. Overall, the desiccation sensitivity trait has also been linked to more easily measured soft traits. It was found that desiccation-sensitive seeds are usually larger, rounder, have relatively lower seed coat ratio and lower surface area per volume ratio (Hong and Ellis, 1998; Daws et al., 2006).

It is also important to highlight the existence of synergy among early-life stages which has to be taken into account when making

projections of species distribution in future climatic conditions using process-based models. The key to the existence of this synergy among effects of water stress on different early life stages is that water stress does not always cease the developmental processes at a certain stage (e.g. gametophyte sterility) and can be carried over to the next. For example, drought induced changes of female gametophytes can result in zygote abortion several days after fertilization (Westgate and Boyer, 1986). Moreover, reduced accumulation of seed reserves that occurs during the water deficit can translate into increased drought sensitivity of seedlings. Drought during the seed stage is known to decrease the seed size which is positively related to the size of cotyledon and embryo. Seedlings emerged from smaller seeds usually develop lower above- and below-ground biomass, have smaller total leaf area and slower initial growth rates (Hendrix and Trapp, 1992). Their shallow root systems make them more vulnerable to the reductions in water supply and suppress their competitive advantage. Although this effect is usually more pronounced at the beginning of the seedling stage, it still can have a significant effect on species establishment. Synergy between seed and seedling stages can occur even if dehydration started only during the phase of seed germination (seed stage). Seeds exposed to severe water stress during germination will likely use more reserves to cope with unfavorable conditions and invest less energy into root production (Boureima et al., 2011). Less developed and shorter root system, in its turn, will prevent proliferation in deeper soil profiles decreasing water uptake and lowering plant's chances of survival during limited water supply (Lloret et al., 2009). Although these synergistic effects have been previously observed, they are rarely taken into account when making predictions of species distribution changes.

5. Ways to incorporate drought sensitivity of early life stages into plant Species Distribution Models

5.1. Correlative and process-based modelling approaches

Although water balance has long been integrated into plant models as an important driver of biomes, plant functional types and plant species distribution (Neilson, 1995; Foley et al., 1996; Hickler et al., 2006, 2012), it is still described in a rudimentary way in species distribution models (SDMs). We can distinguish two different categories of SDMs: correlative SDMs and process-based SDMs (see for review Dormann et al., 2012). Correlative SDMs are based on fitting statistical relationships between environmental drivers and species presence (and sometimes absence). In correlative models, parameters have usually no *a priori* defined ecological meanings and processes are implicit. Process-based models, by contrast, are built around explicitly stated mechanisms and causal relationships between species presence and environmental variables. Moreover, parameters used in process-based models have a clear ecological interpretation defined *a priori*. In this category of models, causal relationships are frequently obtained from the experimental work in contrast to empirical relationships used in their correlative counterparts. Consequently, process-based models often require a larger number of parameters to be estimated or measured, and have a higher level of complexity than the correlative ones. However, they provide greater insights into the drivers that govern species distribution. So far, these two types of models do not integrate the effect of drought stress on reproduction, mostly because they, actually, do not integrate reproduction at all (but see Chuine and Beaubien, 2001), and very few of them integrate the effect of drought stress on early life stages.

From our review, it appears that there are four main missing components that require further development in the latter models: seed production, germination, seedling emergence success, and juvenile survival. In the following, we provide some ways forward of integrating these effects into correlative and process-based models.

5.2. Improving process-based models

We are not aware of models that simulate seed production apart from crop models that can be deployed at large spatial scales and take into the account the effect of water availability on seed yield (Boote et al., 1996; Iizumi et al., 2009; Steduto et al., 2009). Very few SDMs and, more generally, models for non-cultivated plants simulate reproduction processes such as flowering, fruit maturation date, fruit growth, germination date and success. Models that have gone farthest in this direction are individual-based models (IBMs), forest gap models (see for review Vacchiano et al., 2018) and the SDM Phenofit (Chuine and Beaubien, 2001). In these models, seed production has been implemented either as a constant process (Price et al., 2001), as a relative proportion of maximum fecundity varying with environmental conditions (Chuine and Beaubien, 2001), or more mechanistically as a function of net primary productivity (NPP) or leaf mass and resource allocation (e.g. Bossel, 1996). There are not so many models, however, that take into account masting and it is reasonable to say that it is rather an overlooked process in models of plant dynamics and/or phenology (Vacchiano et al., 2018). This occurs mainly because the mechanisms involved in year-to-year variations in fecundity are still poorly understood and the data on fructification are scarce, especially for forest trees (Gallinat et al., 2015). Improvement of models will therefore require beforehand increased efforts in experimental work and data acquisition on fructification.

Although, process-based models of germination and seedling emergence exist since the 1990s (see for review Forcella et al., 2000), most of them were developed for weeds and still have not been integrated into SDMs (but see Manso et al., 2013; Midmore et al., 2015). Incorporating germination and seedling emergence models into process-based SDMs would be a reachable first step towards taking into account the impact of temperature and drought on the early life stages. Germination and seedling emergence models can have different level of complexity. Simpler versions rely on the hydrothermal time concept, i.e. cumulated time exposure to soil temperature and soil water potential above specific thresholds. To implement such models, one also needs to determine specific hydrothermal time curves for each species or population, using data obtained under controlled laboratory conditions. To achieve more complex germination and seedling emergence models, one would additionally need to take into account the impact of seed burial depth, oxygen deficiency, light quality, diurnal soil temperature fluctuations (Forcella et al., 2000). Nonetheless, such level of complexity might be more useful for crop models than for SDMs.

For tree species, the only process-based models considering the impact of the environment on juvenile stages are gap models, but their representation of this impact is still very crude, since they usually simply use specific thresholds of temperature and light (Bugmann and Cramer, 1998; Lischke et al., 2006). Other mechanistic gap models, such as the SIERRA model (Mouillot and Lavorel, 2001), simulate juvenile shoot and root growth, as well as daily water uptake and can estimate differential juvenile mortality rates related to drought. However, they do not take into account differentiated microclimatic conditions (especially temperature and relative humidity) for different vegetation layers, which can be an issue especially for the seedling layer (0–50 cm).

5.3. Improving correlative models

Improving the representation of water availability impacts on reproduction in correlative SDMs might seem more limited. However, a better understanding of these impacts should assist in the selection of meaningful environmental covariates used in the models. One way to incorporate additional biological complexity into correlative SDMs could be by fitting separate model for separate life stages, as the pioneering work of Bell et al. (2014) has proven to be feasible. This approach should facilitate the identification of meaningful environmental

covariates as well as predictive functional traits. Although it will require presence-absence data for different life stages, sharing information across species/populations might allow to overcome this limitation. Another solution, though maybe less powerful, could be using species- or population-specific functional trait values that explain and predict interspecific or inter-population differences in species responses to water availability. Rüger et al. (2012) showed that growth patterns may be predicted with easily measurable morphological traits. Considering the variation of these traits between populations, one might be able to fit correlative SDMs for each population showing specific trait values. In other words, it might be possible to segregate different populations inside a species range using trait variation, and to fit one model per population, assuming that each population behaves differently due to different trait values.

5.4. Common challenges

The major challenge faced by both correlative and process-based SDMs might lie in the ability to accurately simulate soil temperature and water potential. This requires modelling microsite conditions, which could be a technical challenge for models used at continental scales. However, it is becoming increasingly evident that microclimate has a large influence on the current distributions of species and their possible responses to climate change (Potter et al., 2013; De Frenne et al., 2013; Harwood et al., 2014). Modelling microsite conditions has already been used in animal process-based SDMs, particularly for insects, reptiles and amphibians, for which micro-climatic conditions are crucial to explain their presence or absence (Kearney and Porter, 2004, 2009; Regniere et al., 2012; Crespo-Pérez et al., 2011). Incorporating modelled microsite climatic conditions has also been recently achieved to improve the modelling of seedling recruitment in wheat (Bullied et al., 2014a, 2014b). Over the last couple of years, microclimate modelling has also become an issue for correlative models, especially when it comes to addressing the question on the role of micro-refugia - a hot topic in ongoing research (Hannah et al., 2014; Keppel and Wardell-Johnson, 2015). Lenoir et al. (2017) recently proposed methods for modelling the climatic component of potential micro-refugia at very fine (< 1 m) resolutions (e.g. canopy cover). They showed that incorporating high spatial resolution climatic conditions into correlative SDMs increases the predicted probability of local persistence and influences species capacity to adapt to climatic changes.

To improve predictions of terrestrial vegetation response to drought it is crucial not only to increase the complexity of SDMs, but also to enable their fast parameterization. In the case of correlative SDMs, increased complexity does not usually affect their parameterization, except for cases with very rare endemic species with extremely limited presence/absence data (Virgili et al., 2018). In the case of process-based models, however, this depends on the ability to obtain empirical data for as many species as possible. This can be achieved by direct 'forward' parameter estimation using laboratory and field-based experiments and observations which can take several years for a couple of species. Evans et al. (2016) proposed to address this challenge by using hierarchical and inverse modelling. In this case, prior information on the drought sensitivity of key reproductive processes can be used to constrain the parameter estimates. However, recent comparisons between correlative and process-based models showed that forward parameter estimation in process-based models (in opposition to inverse modelling) is a non-negligible part of their robustness (Asse et al. submitted).

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